Dispersal and Abundance of *Lygus hesperus* in Field Crops

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ABSTRACT To predict *Lygus hesperus* Knight population dynamics in the field, a quantitative understanding of dispersal is needed. *L. hesperus* is a major pest of cotton and other seed crops in the San Joaquin Valley. Mark recapture experiments were performed that measured movement and abundance of *L. hesperus* in cotton (*Gossypium hirsutum* L.), alfalfa (*Medicago sativa* L.), and blackeye bean (*Vigna sinensis* L.). Male *L. hesperus* moved farther than females (4.6 versus 3.6 m/d). Movement was greater in the east-west axis than the north-south axis (7.0 versus 2.4 m/d). Calculations based on mark–recapture data suggest that a random walk model describes *L. hesperus* dispersal well. Diffusion estimates predict 98% movement radiuses in cotton, alfalfa, and bean as 15.6, 14.4, and 7.3 m/d, respectively. Estimates of absolute *L. hesperus* abundance were 45,000/ha in alfalfa during the August peak, approximately five times those in cotton. The results suggest that management of *L. hesperus* may be affected by greater dispersal along the east-west axis and the strong male bias in sweep-net samples.

KEY WORDS dispersal, pest management, mark–recapture, western tarnished plant bug

COTTON PESTS AND THEIR natural enemies move within cotton fields and disperse between these fields and adjacent areas. Quantitative knowledge of the movement of *Lygus hesperus* Knight is lacking in the field, although some studies have helped our understanding of dispersal. One study showed that fluorescent dye has no discernable affect on movement behavior (Stern and Mueller 1968) and was used to show that *L. hesperus* moves between alfalfa and cotton fields. Further studies (Sevacherian and Stern 1972, 1974, 1975) showed *L. hesperus* preference for alfalfa and the accumulation of marked bugs in alfalfa when released in nearby cotton. A better understanding of dispersal by *L. hesperus* is needed to support integrated pest management (IPM) efforts. This study characterizes movement and abundance of *L. hesperus* in the field.

Lygus hesperus plays a pivotal role in cotton pest management. In U.S. cotton, *Lygus* bugs caused $37 million in control and yield loss in 2002 (Williams 2003). *L. hesperus* has the largest economic impact of any cotton pest in California, with an estimated yield loss of 42,000 bales in 2001 (CDFA 2002). *L. hesperus* is controlled with broad-spectrum insecticides that can deplete the natural enemy complex and cause outbreaks of secondary pests.

A specific objective in this study was to measure *L. hesperus* dispersal distance in row-crops known to be host plants. The combination of capture–mark–recapture and diffusion models have been shown to be effective for measuring insect dispersal (Turchin and Thoeny 1993, Turchin 1998). An advantage of this technique is the ability to predict dispersal, and the null form for diffusion may be amended to account for sex differences and directional bias (cardinality). *L. hesperus* shows peak activity in the evening, especially near dusk (Mueller and Stern 1973). This periodicity in response to environmental cues would seem to suggest nonrandom movement because of daily patterns of resource availability. The daily variation in activity may influence flight behavior and cause heterogeneity in dispersal distances or direction (Ovaskainen and Cornell 2003). Insects are known to exhibit directed movement in response to preferred host plants (Sevacherian and Stern 1972) and alter their movement behavior in response to canopy complexity (Kareiva 1982, Margolies 1993). Mark–recapture experiments were used to measure the rates of dispersal and examine the factors that govern movement.

Another objective was to acquire absolute estimates of *L. hesperus* abundance in the field. Knowledge of potential population density may inform the scale of scouting for *L. hesperus* as it moves among field crops. The ability of *L. hesperus* to move long distances without regard to the availability of host plants could impede management at the field scale. However, high abundance on preferred plants may suggest an arrestment response (Kareiva 1983) and function as a trap crop. If dispersal rates are high enough that *L. hesperus* frequently encounters field borders, abundance on preferred plants would be important for arresting *L.*

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hesperus and keeping them out of cotton fields during the vulnerable period of square formation. This gap in our knowledge inspired the measurement of movement distance, direction, and absolute abundance in cotton, bean, and alfalfa fields.

Materials and Methods

Mark–release–recapture experiments were performed in cotton (*Gossypium hirsutum* L.), alfalfa (*Medicago sativa* L.), and blackeye beans during 2003 and 2004 (*Vigna sinensis* L.). All experiments were conducted in fields near Shafter, CA. In 2003, experiments were performed at the University of California Research Extension Center in Shafter (SREC). Weather data were recorded by a California Irrigation Management Information System (CIMIS) station at SREC, and weather during all experiments was sunny and warm, with an average or 26.2 ± 1.9°C (high of 39.0°C and low of 12.3°C). Wind was also mild during the experiments, averaging <1.3 ± 0.17 km/h, and wind direction was predominantly from the northwest. The first year, marking and mortality studies were conducted in cotton and alfalfa. In 2004, experiments were performed at SREC in cotton and blackeyed bean fields, and another site was used about a mile from the station, in an alfalfa field. Over both years, one field of bean and two separate fields of alfalfa and cotton were used. No insecticides were sprayed on any field site for at least 4 mo before the study.

Insects were collected from an alfalfa field with a sweep net and brought to the laboratory in a large cage. *L. hesperus* were separated from other insects using an aspirator and weighed to estimate their numbers. *L. hesperus* adults were marked with a fluorescent dye and held in a cooler until released in the late afternoon. Insects were released at a central point in a trapping web design and recaptured at regular intervals of space and time. Releases were made Monday through Wednesday with different colored dyes, and recapture samples were taken Tuesday through Saturday.

Mark and recapture methodology used the point release technique during the 2-yr study (Turchin and Thoeny 1993). During the first year, releases were performed in one cotton field during July and early August, when cotton was flowering. Releases were also made on the edge of a cotton field and next to an alfalfa field. These releases occurred from late July to the end of August, when cotton was forming squares and bolls. These recaptures were excluded from testing of variability in cardinal direction of dispersal because of the bias that the north–south border may impose on movement. In the second year, recaptures were made for trapping webs in the central portion of each cotton, bean, and alfalfa fields. Beans were fully grown with pods in July, but had a relatively small canopy compared with alfalfa or cotton. Alfalfa was between 40 and 60 cm in height during the experiments. Finally, cotton plants were between 80 and 120 cm in height during the experiments. Although, the study was limited to annual availability of a single field of each crop, the uniform stands in each of the fields suggested variation in results was minimally affected by unique soils or agronomic practices.

In all releases, sweep-net sampling was located at 1.8, 4.9, 10.1, 20.1, and 30.5 m from the central release point. At 1.8 and 4.9 m, two cardinal directions were sampled. At 10.1 and 20.1 m, four cardinal directions were sampled, and at 30.5 m, eight cardinal directions were sampled. Sweep net samples were taken at ≈1000 h each morning. The number of sweeps was 6, 12, 18, 24, and 30 as the distance from the central release point increased. The increase in sampling effort at greater distances prevented depletion at closer distances and balanced the sampling per unit of area further from the release point.

Lygus hesperus captured in a sample location were placed in a paper bag and brought to the laboratory before analysis. Sample bags were frozen to kill captured insects. Marks were verified by illuminating the leg articulations where fluorescent powder was held. Transfer of marks to unmarked individuals was also prevented by examination of crevices in the cuticle around the legs. Each captured *L. hesperus* was recorded by sex, sample location, and whether they were marked.

The first method used statistical testing with a general linear model to determine variables influencing movement. The second analysis used a variation of the diffusion model to account for differences caused by crop plant, direction, and sex (Turchin 1998). A hypothesis was that there would be differences in movement among the field crops and cardinal directions from the release point. The final analysis provided an estimate of absolute abundance of *L. hesperus* in the fields.

Analysis of Variance. Analysis of variance (ANOVA) was used to test key assumptions before a dispersal estimate was made. The distance that each marked insect traveled was the response variable, and sex, crop type, direction, and day since release were the indicator variables. The distance was natural log transformed [$\ln(r)$]. The statistical model used categorical variables for sex, crop, and direction and treated time since release as a regression variable. The distance of recaptured *L. hesperus* was analyzed in a general linear model. Recapture samples were eliminated for bugs that were captured along diagonal axes or in traps not balanced along the four cardinal directions. Directional comparisons for distance along a cardinal direction were made using Tukey's unbalanced honestly significant difference (HSD) test, and comparisons of the number of insects caught along directional axes were made using the nonparametric Kuskal-Wallace test (StatSoft 1999).

Diffusion. The frequency histograms of the dispersal data were analyzed with a diffusion approximation, which estimates dispersal. Each frequency histogram over distance was fitted with equations based on the assumption of a random walk. The random walk model assumes undirected movement of individuals (Okubo 1980). Only recaptures made on the first 3 d after release were used in analysis because this afforded each released insect an equal probability of being caught. Although some *L. hesperus* were recaptured after 3 d, these data would be biased by the unbalanced recapture opportunity for each insect. The simplest form of the random walk model predicts population density based on the diffusion coefficient (D).

$$\partial u / \partial t = D \partial^2 u / \partial r^2$$

where u is population density, t is time in days since release, and r is radial distance from the release point. The simple random walk model may be adjusted to account for violations of assumptions discovered in the ANOVA. This model estimates the frequency of a population using the following assumptions. (1) Marking does not affect the insects in movement or mortality. The mortality assumption was tested by holding 50 marked and 50 unmarked *L. hesperus* in individual vials for 6 d in the laboratory. A total of five marked and four unmarked insects died, which was nonsignificant (df = 98; $t = 0.35$; $P = 0.73$). (2) Another assumption is that there are no differences in movement between male and female *L. hesperus.* (3) An additional assumption is that the insects do not move preferentially in one direction from the release point, also called cardinality. (4) Finally, the standard model assumes a random walk in a uniform field, which is always violated to some degree. Even in the monoculture row crops used in this study there may be variation in plants because of soil, watering regimen, or other agronomic practices. We applied a time-dependent model (Turchin 1998), which has the following solution for the two-dimensional diffusion equation in discrete form.

$$N(r,t) = N_0 / (4\pi Dt) \exp[-r^2/(4Dt)]$$

where N represents the number of recaptures at a given distance (r) and time (t). N_0 is the number released and D is as in Eq. 1. The value of D is solved by iteration to minimize squared error (method of least squares). The dispersal frequency histogram may be divided into subsets to compare differences among crop hosts (Ovaskainen and Cornell 2003).

Dispersal distances may be estimated with the diffusion coefficient. The distance that encompasses 98% of the bugs is:

$$r_{98} = 2\mathrm{sqrt}(4Dt)$$

where all variables are as described above (Okubo 1980). This measure for each of 3 d provides an intuitive measure to compare dispersal from different categories (e.g., crops).

When unexplained variation in movement is aggregated in a frequency histogram, the distribution becomes leptokurtic (Morales 2002, Ovaskainen and Cornell 2003). An equation developed by Taylor (1978) and Nathan et al. (2003) was used to measure the width of the tail in the histogram. This function was used to calculate the shape of the tail of dispersal distributions. The equation for probability distribution of dispersing organisms (P),

$$P = c / [2a\exp(\mathrm{gammainv}(1/c)] \exp[-(r/a)^c]$$

where r is the distance from the release point, a is a fitted dummy parameter, and c is the parameter determining the distribution's shape. When $c > 2$, the distribution is normal and fits the random walk assumptions. When $1 < c < 2$, the distribution has an exponential shaped tail. When $c < 1$, the distribution is leptokurtic and suggests nonrandom or directed movement.

Abundance. The analysis estimated the absolute abundance of *L. hesperus.* The Lincoln index (Bailey 1952) is a variation of the Jolly-Seber method that is more stable for small samples.

$$N = M(A + 1)/(R + 1)$$

$$SD(N) = \mathrm{sqrt}[M2(A + 1)(A - R)]/[(R + 1)2(R + 2)]$$

where N is the population estimate, M is the number of marked bugs, A is the number of unmarked bugs, and R is the number of recaptured bugs that were marked. The estimates are robust because they depend on the ratio of marked to unmarked insects and removes bias because of capture efficiency. Separate estimates of abundance were calculated in each field and each year. The approach assumes that mortality was negligible during the interval from release to recapture. The daily mortality rates were likely to be in the range of 6% per day (personal observation), and survival up to a month has been observed (Leigh 1963, Bryan et al. 1976, Cave and Gutierrez 1983). The effect of distance was accounted for by pooling recaptures across distance for each week. To account for variation in number of weeks that the trials were performed in different fields, the total captures of unmarked bugs were divided by the number of weeks that experiments were performed. This was needed to balance the sampling effort used to acquire *L. hesperus.* Separate population estimates were made for each recapture web.

Results

Approximately 17,490 marked *L. hesperus* adults were released, and a total of 626 marked bugs were recaptured. The recapture data showed a male sex bias of 1.15 (m:f: $\chi^2 = 3.0$; df = 1,611; $P = 0.08$), whereas the capture of unmarked *L. hesperus* showed a significant male sex bias of 1.62 (m:f: $\chi^2 = 24.3$; df = 1,812; $P < 0.01$). Although it is not clear whether a natural sex bias exists in the field, the results show greater ability to trap males using a sweep net.

ANOVA. Analysis of dispersal distance showed the effect of sex, direction, and time since being released (Table 1). Days since the release was significant, as expected, and showed a steady mean increase in dispersal distance over time. Tukey's (StatSoft 1999) test for within-group differences showed *L. hesperus* dispersed farther when released in cotton than bean ($P < 0.05$; Fig. 1a), and dispersal of insects released in alfalfa was intermediate, not significantly different from cotton or bean. In addition, males dispersed significantly farther than females ($P < 0.05$; Fig. 1b). Finally, dif-

Table 1. ANOVA for distance moved by each recaptured *L. hesperus*

	df	Sum of squares	F	P
Intercept	1	983.4	2129.5	<0.01
Direction	1	157.2	340.4	<0.01
Day	1	14.3	31.0	<0.01
Sex	1	8.91	19.4	<0.01
Crop	2	3.7	4.0	0.02

All variables were significant indicators in the general linear model (R^2 = 0.42).

ferences in movement distance were significantly different among cardinal directions ($P < 0.05$).

A further test of directional bias in dispersal was conducted using Tukey's test that showed homogenous groups along one axis of movement (df = 603, $P <$ 0.05). Average daily movement distances north and south were 2.42 and 2.44 m, respectively, whereas movement distances east and west were 6.94 and 7.15 m, respectively. The movement bias for longer dispersal in the east/west axis over the north/south axis was not evident in the number of recaptures among cardinal directions (Fig. 2a and b). We hypothesized that movement was influenced by some combination of the orientation of rows, solar track, or prevailing wind. Rows were oriented along the north-south axis in cotton and bean fields, while alfalfa was grown in a uniform stand, without rows. The interaction of crop and direction was not significant (F = 0.40; df = 6; P = 0.66). This effectively eliminated the importance of row orientation because alfalfa should have shown an interaction, but it also showed an effect of the cardinal direction. Figure 2b shows the recapture counts by cardinal direction. This shows a significant effect of cardinal direction based on the Kruskal-Wallace test (H = 9.22; df = 3,12; P = 0.03). Multiple comparisons within direction showed nonsignificant, lower recaptures in the east direction than the west (P = 0.08) and north (P = 0.08). These results were further examined with nonlinear dispersal functions.

Diffusion. The ANOVA indicated that the data should be split by each crop, sex, and directional axis. The split created 12 frequency histograms (three crops, two sexes, and two axes). The diffusion equation (equations 2 and 4 were fitted to the 12 distributions; Table 2).

Two of 12 categories (9 and 12) fit an exponential dispersal distribution more than a normal random walk. The rest of the categories fit random walk dispersal assumptions, and none were more leptokurtic than the exponential fitted tail.

The fit of diffusion equations showed an overall average dispersal of ≈12.5 m/d by *L. hesperus* (Table 2). In mid-season cotton, movement rate was 15.8 m/d. In alfalfa, *L. hesperus* did not move as much, with predicted movement of 7.3 m/d. Average dispersal prediction was greater for males than females (9.9 and 8.1 m/d, respectively). The strongest effect was seen in the average rates of movement along directional axes, as insects moved six times the distance along the east/west axis compared with the north-south axis (9.5 versus 1.8 m/d).

Abundance. Abundance estimates were made for each field (Table 3). Abundance of *L. hesperus* was largest on alfalfa sampled in 2003. This field had large numbers of endemic *L. hesperus*, which were at peak seasonal abundance during August. *L. hesperus* preference for alfalfa over cotton was clear because of the relatively low numbers in edge-cotton. Marked and released *L. hesperus* were recaptured in alfalfa at five times the rate in cotton. The cotton fields showed consistent estimates in both years. Finally, blackeyed beans harbored the lowest abundance, which may be related to the relatively small canopy and profile of the plant.

Discussion

Several results were surprising. The large effect of directional axis on *L. hesperus* movement distance was unexpected. However, if *L. hesperus* responds to the direction of light, their crepuscular behavior provides an intuitive explanation for the directional bias observed. A recent study found a strong phototactic response by *L. hesperus* using a photodiode (Blackmer et al. 2004). The effect of wind may also play a role as inferred from the greater recapture counts toward the northwesterly prevailing winds. However, Mueller and Stern (1973) measured the greatest activity in the evening, so *L. hesperus* may simply be positively pho-

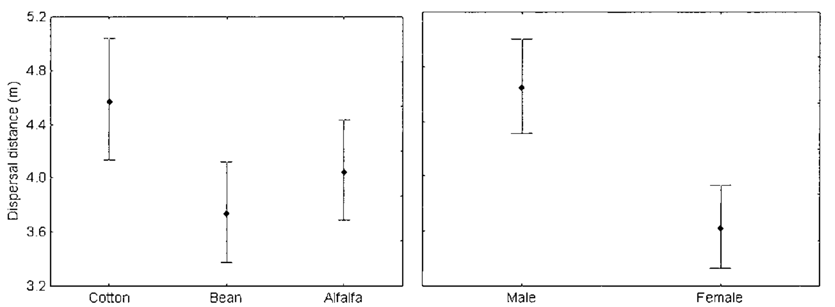
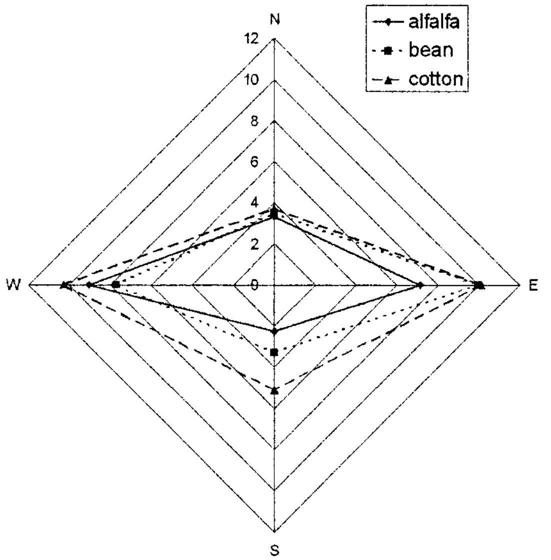


Fig. 1. Daily movement distance from least squares of ANOVA by (a) crop and (b) sex. *L. hesperus* males showed greater daily movement, especially in cotton fields.



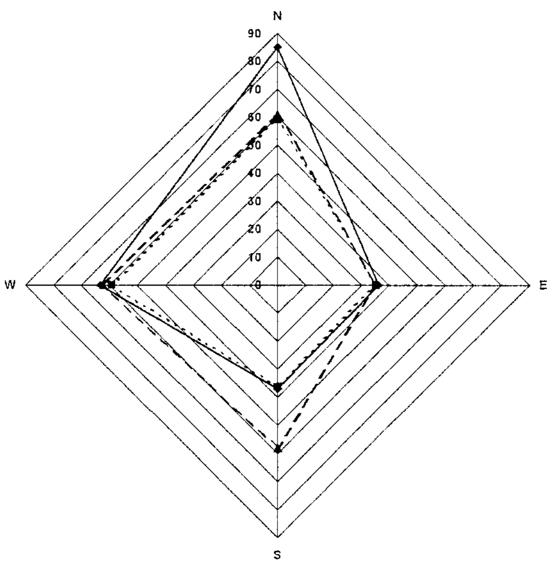


Fig. 2. Daily movement according to cardinal direction. (a) The average distance (meters) moved by recaptured *L. hesperus*. (b) Number of *L. hesperus* moving in each direction. Distance of movement was greatest along the east-west axis, which is coincident with light orientation at dawn and dusk. Abundance of captures was greater to the north and west than the east, which seemed to correspond to prevailing wind from the northwest.

totactic. Our estimates of dispersal distance, although slightly different, showed more consistency among crops and sexes. There were also consistent predictions of abundance in cotton. As expected, time of year (season) resulted in large population differences in alfalfa fields. The results also suggest that beans, despite the low abundance and relatively small canopy of bean plants, are the preferred host of *L. hesperus* compared with alfalfa and cotton. They moved most slowly through beans, which is suggestive of arrestment behavior (Kareiva 1983).

Table 2. Key parameters resulting from fitting the phenomenological model of Nathan (2003) and diffusion model

Sex	Crop	Axis	c[a]	r98[b]
Female	Alfalfa	East/west	32.6	23.9
Female	Alfalfa	North/south	2.3	3.2
Female	Bean	East/west	38.2	18.0
Female	Bean	North/south	2.8	3.4
Female	Cotton	East/west	24.2	15.2
Female	Cotton	North/south	3.0	3.1
Male	Alfalfa	East/west	48.8	27.2
Male	Alfalfa	North/south	3.4	3.3
Male	Bean	East/west	1.4	4.7
Male	Bean	North/south	2.2	3.3
Male	Cotton	East/west	32.3	37.5
Male	Cotton	North/south	1.8	6.6

[a] c is the parameter determining the shape of the fitted equation.
[b] r^{98}represents the distance (meters) encompassing 98% of dispersing *L. hesperus*.

Dispersal was quite variable among categories. There was very low dispersal by females in the north-south axis, especially in alfalfa. Alternatively, movement by males along the east-west axis would suggest emigration from cotton fields within a couple days. The movement of *L. hesperus* outside of these host crops is likely to be greater because host plants would not arrest movement behavior. *L. hesperus* has a host range of over 100 plants, but the crops chosen in this study are preferred host plants in the San Joaquin Valley (Scott 1977). This study supports the management of *Lygus* in cotton by assigning a damage risk based on the specific plant distributions surrounding the field of interest (e.g., Goodell et al. 2000).

Dispersal differences among crops may have biased estimates of absolute abundance. Usually, efforts in marking studies are designed to acquire as many recaptures as possible while observing all distances of movement (Seber 1995). In this study, we increased sampling effort with distance from the release point. This prevented early recapture or "trapping out" (Turchin and Thoeny 1993) of *L. hesperus* near the release point, and allowed us to record events of longer distance dispersal. However, a simple estimate of sampling area shows we sampled proportionally less area as we increased the radius from the central release site. Basically, the proportion of area in successive annuli of the recapture web increased faster than the sweep effort used at increasing distances. This suggests that estimates of abundance in crops with lower dispersal, bean and alfalfa, may be overestimated. The opportunity for capturing *L. hesperus* was reduced as they became disproportionately diluted further from the release point. In this study, the dispersal distances in all crops were low compared with the farthest recapture distance. Therefore differences in dispersal distances among crops were unlikely to have large effects on abundance estimates.

An interesting assumption to test is the effect of host–plant conditioning on movement. Recent studies show that hungry *L. hesperus* may cause greater dam-

Table 3. Estimates of absolute abundance

Field	Abundance per acre	Abundance in sampling web	SD	Marked *L. hesperus* released	Recaptures	Unmarked captures	Weeks sampled
Alfalfa edge[a]	45,464	88,000	7,286	4,500	20	1,211	3
Cotton edge[a]	1,605	3,107	1,188	4,500	53	207	3
Cotton[a]	7,716	14,936	3,492	3,546	10	128	7
Alfalfa[b]	4,862	9,410	23	5,069	201	346	2
Bean[b]	5,605	10,849	26	7,749	189	152	2
Cotton[b]	7,588	14,688	846	7,140	153	814	5

Cotton held a consistent abundance of *L. hesperus* in mid-season between years. Alfalfa held much fewer *L. hesperus* when examined in late season, September 2004.
[a]Performed in 2003.
[b]Performed in 2004.

age than transient bugs simply migrating through a field (Zink and Rosenheim 2004). In this study, all marked *L. hesperus* were originally collected from alfalfa. Insect physiological changes induced by the host plant may manifest in differing levels of damage that a single bug can inflict when feeding on cotton. Future experiments could be designed to discern the behavioral and physiological mechanisms controlling damage to cotton plants. Cotton is known to be most vulnerable during square-set (flower bud) in mid-season, but the availability of *L. hesperus* forced this study to occur in the latter half of the growing season. Similarly, we were constrained to use *L. hesperus* from alfalfa fields, but this may have influenced their relative movement rates within the field crops examined in this experiment. Alfalfa acreage and field density makes it the dominant host in the southern San Joaquin Valley during summer months. The problem of mass emigration by *L. hesperus* from a cut alfalfa field gives credence to the importance of measuring dispersal rates (Sevacherian and Stern 1974, Fleischer et al. 1988).

The inferences about *L. hesperus* movement in other fields of beans, alfalfa, and cotton may be affected by locally representative insects and field conditions. Resource limitations prevented using separate field sites for each of the 22 release trials, but the farm crew made great efforts to use common agronomic practices so fields were uniform and similar to regional grower's fields. In addition to field characteristics, the use of local population *L. hesperus* also imposes limitations on extrapolating to all populations or to other *Lygus* species. The idiosyncrasies of local conditions undoubtedly introduces some bias to the results.

A method to recapture all insects without bias for a given canopy area would improve the generality of the mark–recapture methods used here. Crop canopy poses a difficult issue for assessing how *L. hesperus* perceive the size of an area. The complexity of the large cotton canopy found in the San Joaquin Valley clearly represents more habitat area than the canopy of bean plants. Sampling whole plants for *L. hesperus* is difficult because they readily take flight (Leigh et al. 1970). The circadian behavior of *L. hesperus* may result in systematic variation if sampling is not performed at the same time each day (Butler et al. 1971, Rancourt et al. 2000). This study took care to make sweep samples at the same time each day, so movement along the east/west axis was not an artifact of the methods (Fig. 1). *L. hesperus* seemed to be orientating to the wind or, perhaps more strongly, to the sun.

The distance that *L. hesperus* move each day does not suggest long distance migration during the time frame of these experiments. This is an advantage for the scale needed to manage *L. hesperus* because only the surrounding fields may be required to provide satisfactory IPM. However, this conclusion is contingent on movement behaviors that do not change drastically with *L. hesperus* age, which was not controlled in this experiment.

The impact of the natural enemy community on population density of *L. hesperus* may be underappreciated. Further study will evaluate the relative scales of predator and parasite movement. Quantifying the effectiveness of natural enemies would be important for evaluating cultural management alternatives, including strip-cropping (Stern and Mueller1968), barrier hedges (Bergelson and Kareiva 1987, Jackson et al. 1998), and flowering nectar sources (Landis et al. 2000). Differential movement of parasitoids and their response to plants may have implications on choosing parasitoids and their release techniques for IPM. Finally, knowledge of *L. hesperus* dispersal to and from cotton will form the basis for investigation of *L. hesperus* forecasting and management using remote sensing and climatic data.

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